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## Analysis of Variability in Home-Range Size of the American Marten

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## ANALYSIS OF VARIABILITY IN HOME-RANGE SIZE OF THE AMERICAN MARTEN

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**Abstract:** We investigated measurements of home-range size of the American marten (*Martes americana*) (based on telemetry and the minimum-convex-polygon methods) from the literature for sources of variation. Male home-range size varied significantly among study sites, but female home ranges did not. Home ranges of males were larger than those of females. Mean home-range size did not vary significantly with number of radio locations, or with sampling interval. Sample duration was a significant source of variation in home-range size. Home-range size was not significantly correlated with geographic latitude or with mean annual temperature range. Between-site differences emphasize the need for identifying ecological factors that may explain variability in sizes of marten home ranges.

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The concept of home range (Burt 1943) has been interpreted as a life history variable (home-range size) that has been reported for mammalian species (Harestad and Bunnell 1979, Eisenberg 1981) and functionally related to a wide range of life history traits (Harestad and Bunnell 1979, Calder 1984, Lindstedt et al. 1986). Increasingly, site-specific home-range size is used as a basis for population estimation in territorial Carnivora (Berg 1979, Thompson and Colgan 1987). However, in studies of some carnivores, estimates of home-range size that reflect local

conditions have been difficult to obtain because of high within-site variability in space requirements. Laundré and Keller (1984) found no differences in mean home-range size of coyotes (*Canis latrans*) among 4 geographic areas representing distinct habitats. This suggests that between-site differences in coyote home-range sizes are obscured by other sources of variation, such as within-site variability in prey densities or habitat use. Large within-site variation in home-range size also could be due to ecological and social plasticity of coyotes (Gier 1975), increas-

ing within-site variation in patterns of habitat use and thereby obscuring individual space requirements. Laundré and Keller (1984) also found no differences in home-range size attributable to sex or social status. This lack of site, sexual, and social differences in coyote home-range size appears to limit the use of this variable in testing hypotheses about resource conditions for coyotes.

The American marten differs from the coyote in several life history characteristics suggesting that marten should exhibit greater between-site variation in home-range size than coyotes. The marten is a habitat specialist, largely restricted to conifer-dominated forest stands (Allen 1984). The marten is reproductively frugal for its body size (Markley and Bassett 1942), consistently asocial in its nonbreeding dispersion (Strickland et al. 1982), and exhibits no direct paternal care of young (Kleiman and Malcolm 1981). We analyze possible causes of variation in reported home-range sizes of the American marten. We discuss the value of home-range studies of marten and suggest ways that these can provide better understanding of the ecological significance of home-range size.

We are grateful to a number of researchers who provided information supplemental to their published accounts, which made our analyses possible. J. A. Bissonette provided data on sampling durations and weights of telemetered marten in Newfoundland. M. K. Brown provided data on home ranges of telemetered marten in New York. M. C. Bateman provided body weights for marten she studied in Newfoundland, and R. H. Jessup provided data on sampling durations of marten in Yukon Territory. This study was supported by the Wyoming Game and Fish Department.

## METHODS

We obtained estimates of marten home ranges from the literature (Table 1). Estimates for animals considered non-resident or transient, and therefore not possessing true home ranges (e.g., non-residents [Burnett 1981]), were excluded from the analysis. To minimize measurement sources of variation, we used only home ranges based primarily on telemetry, although several authors included trap captures with a larger number of telemetry locations. We also limited our analysis to home ranges in which the perimeter was depicted by a minimum-convex-poly-

gon (Mohr 1947) or related technique (Harvey and Barbour 1965, Mohr and Stumpf 1966, Southwood 1966). Latitudes, longitudes, and elevations for study areas were means of reported values or estimates from large-scale topographic maps. Mean annual temperature range (Steinhauser 1979) was used as an index of seasonality of study sites. Body weights for individual animals were means of all values reported for study periods. Animals  $\geq 1$  year old were considered adults; younger animals were juveniles.

In our model for variation in home-range sizes, we identified 2 potential sources of variation: measurement (sample size, sampling interval, and sampling duration) and biological or ecological factors (environmental conditions, age, sex, and body size). Sample size (the no. locations used to depict a home range) has been shown to have a nonlinear, positive relationship to estimated home-range size (Cranford 1977, Bekoff and Mech 1984) if based on nonstatistical measures such as the minimum convex polygon. The duration over which sampling occurs also may have important effects upon home-range size because home-range coverage and shifting of home-range boundaries occur over time (Buskirk and Lindstedt 1989). Mean sampling interval ( $\bar{x}$  time between locations) was considered a source of variation in home-range size because of possible autocorrelation in samples of locations separated by brief time periods (Swihart and Slade 1985). The effect of these measurement factors was analyzed to control for the effects of sex and study site. Each factor was correlated against home-range size within sex and study site if there were  $\geq 2$  cases in the treatment group, and the signs of the coefficients of correlation compared to expected values (1: 1) with 2-tailed binomial tests. Because of differences in animal numbers studied among the 9 study sites, means of individual characteristics (e.g., body mass, home-range size) were averaged for study sites, and sites used as the units of replication in tests for the effect of study area. Variability of home ranges was compared for juveniles and adults with Levene's test of equality of variances (Dixon et al. 1985:96). Tests for between-site variation in home-range size were conducted by analysis of variance (ANOVA) techniques using sites as the unit of replication. These were followed by pairwise comparisons of home-range size using Duncan's multiple-range tests. Body mass of males and females

Table 1. Home-range sizes of American martens.

Site no.	Location	Elevation (m)	Sex	Age <sup>a</sup>	Body mass (g)	No. locations	Sampling duration (day)	$\bar{x}$ sampling interval (day)	Home-range size (ha)	Source
1	Manit., 51.1°N, 95.3°W	325	M	Juv	1,350	95	223	2.4	1,060	Raine (1981)
1	Manit., 51.1°N, 95.3°W	325	M	Juv	1,100	39	36	0.9	960	Raine (1981)
1	Manit., 51.1°N, 95.3°W	325	F	Ad	660	129	118	0.9	1,250	Raine (1981)
2	Calif., 39.5°N, 120.3°W	2,250	M	Ad	1,015	122	360	3.0	489	Spencer (1981)
2	Calif., 39.5°N, 120.3°W	2,250	F	U	694	42	257	6.3	420	Spencer (1981)
2	Calif., 39.5°N, 120.3°W	2,250	F	Ad	713	56	89	1.6	59	Spencer (1981)
2	Calif., 39.5°N, 120.3°W	2,250	F	Ad	600	38	271	7.3	526	Spencer (1981)
2	Calif., 39.5°N, 120.3°W	2,250	F	Ad	698	298	204	0.7	322	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	F	Ad	637	50	175	3.6	294	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	F	Ad	1,186	216	153	0.7	272	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	M	Ad	1,013	133	48	0.4	297	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	M	U	956	18	44	2.6	537	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	M	U	888	23	43	2.0	380	Simon (1980)
2	Calif., 39.5°N, 120.3°W	2,250	M	Ad	956	13	86	7.2	358	Simon (1980)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,290	97	274	2.9	937	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,470	35	183	5.4	566	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	F	U	950	34	36	1.1	109	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,300	39	86	2.3	448	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,190	42	75	1.8	1,342	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	F	U	1,080	43	91	2.2	2,056	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,250	22	80	3.8	474	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,440	18	83	4.9	544	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,370	32	89	2.9	487	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	F	U	860	36	85	2.4	790	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Ad	1,280	8	18	2.6	598	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	F	Juv	775	11	34	3.4	215	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Juv	1,200	40	156	4.0	722	Buskirk (1983)
3	Alas., 62.8°N, 148.8°W	600	M	Juv	1,085	46	67	1.5	995	Buskirk (1983)
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	901	36	124	3.5	370	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	901	49	55	1.2	520	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	889	42	135	3.3	770	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	900	14	55	4.2	200	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,274	40	135	3.5	870	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,224	21	86	4.3	280	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,352	42	135	3.3	650	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,319	34	86	2.6	720	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	817	30	135	4.7	800	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,141	58	169	3.0	570	Archibald and Jessup (1984)

Table 1. Continued.

Site no.	Location	Elevation (m)	Sex	Age <sup>a</sup>	Body mass (g)	No. locations	Sampling duration (day)	$\bar{x}$ sampling interval (day)	Home-range size (ha)	Source
4	Yukon, 61.2°N, 133.3°W	1,048	F	Ad	765	31	86	2.9	210	Archibald and Jessup (1984)
4	Yukon, 61.2°N, 133.3°W	1,048	M	Ad	1,149	24	64	2.8	590	Archibald and Jessup (1984)
5	Me., 45.5°N, 69.5°W	390	M	Ad	810	272	82	0.3	920	Steventon (1979)
5	Me., 45.5°N, 69.5°W	390	M	Ad	900	93	106	1.2	920	Steventon (1979)
5	Me., 45.5°N, 69.5°W	390	F	Ad	550	53	43	0.8	250	Steventon (1979)
5	Me., 45.5°N, 69.5°W	390	F	Ad	513	12	37	3.4	160	Steventon (1979)
5	Me., 45.5°N, 69.5°W	390	M	Juv	640	557	30	0.1	500	Major (1979)
5	Me., 45.5°N, 69.5°W	390	M	Ad	810	453	34	0.1	1,000	Major (1979)
5	Me., 45.5°N, 69.5°W	390	M	Ad	900	296	97	0.3	780	Major (1979)
5	Me., 45.5°N, 69.5°W	390	F	Ad	550	42	12	0.3	100	Major (1979)
6	Mont., 48.7°N, 114.1°W	1,290	M	Juv	850	16	174	10.9	70	Burnett (1981)
6	Mont., 48.7°N, 114.1°W	1,290	M	Juv	942	22	306	14.6	80	Burnett (1981)
6	Mont., 48.7°N, 114.1°W	1,290	M	U	1,113	5	182	45.5	80	Burnett (1981)
6	Mont., 48.7°N, 114.1°W	1,290	M	Ad	1,092	10	178	19.8	120	Burnett (1981)
6	Mont., 48.7°N, 114.1°W	1,290	F	Ad	663	7	76	12.7	60	Burnett (1981)
7	Minn., 47.7°N, 91.5°W	420	M	U	775	26	95	3.8	1,660	Mech and Rogers (1977)
7	Minn., 47.7°N, 91.5°W	420	F	U	672	10	28	3.1	430	Mech and Rogers (1977)
7	Minn., 47.7°N, 91.5°W	420	M	U	734	18	62	3.4	1,990	Mech and Rogers (1977)
7	Minn., 47.7°N, 91.5°W	420	M	U	1,012	11	61	6.1	1,050	Mech and Rogers (1977)
8	N.Y., 44.2°N, 74.2°W	762	M	Ad	740	118	219	1.9	280	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	M	Ad	775	87	190	2.2	370	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	F	Ad	530	177	194	1.1	170	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	M	Ad	805	266	440	1.7	350	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	F	Ad	430	184	232	1.3	380	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	M	Ad	825	162	265	1.6	770	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	M	Ad	860	177	251	1.4	470	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	F	Ad	370	16	35	2.3	60	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
8	N.Y., 44.2°N, 74.2°W	762	F	Ad	890	69	90	1.3	200	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)

were compared by a paired *t*-test using the site as the unit of replication. Probability values  $\leq 0.05$  were considered statistically significant.

RESULTS

Measurement Sources

Twelve of 15 correlations of home-range size with sampling duration were positive, a significant departure ( $P = 0.04$ ) from 1:1. We identified a single case (a M from Mont. [Burnett 1981]) which when deleted, caused a loss of significance in the relationship between duration and home-range size. With this deletion, home-range size was not significantly correlated with number of locations ( $P > 0.50$ ), sampling duration ( $P = 0.12$ ), or sampling interval ( $P > 0.50$ ).

Biological and Ecological Sources

Body mass was significantly greater for males than for females ( $P < 0.0001$ ). Mean male weights were  $1.5\times$  heavier than those of females. Male home ranges were significantly larger than those of females ( $F = 4.28$ ; 1,8 df;  $P = 0.043$ ). Mean male home-range sizes were  $1.93\times$  those of females. When we controlled for the effect of sex, home-range size varied significantly among 9 study sites ( $F = 4.86$ ; 8,1 df;  $P < 0.001$ ) (Fig. 1), with 15 of 32 pairs of site mean home-range sizes significantly different. Male home ranges varied more among study sites ( $F = 4.42$ , 8 df,  $P = 0.0007$ ) than did female ranges (ANOVA,  $F = 1.60$ , 8 df,  $P = 0.18$ ). Multiple comparisons of male home-range sizes found 12 of 36 pairs of site means significantly different (Fig. 1).

Mean home-range size showed no obvious geographic pattern. When the absolute value of differences between mean home-range size (M only) was correlated with distance between sites, the relationship was not significant ( $r = -0.19$ ,  $P = 0.28$ ,  $n = 36$ ). Mean annual temperature range was not significantly correlated with body mass or home-range size. Site-specific mean body mass was significantly correlated with latitude for males ( $r = 0.73$ ,  $P = 0.025$ ,  $n = 9$ ) and for females ( $r = 0.85$ ,  $P = 0.004$ ). No relationship existed between home-range size and latitude for males ( $P > 0.50$ ) or females ( $P > 0.50$ ). Correlations between longitude and home-range size and elevation and home-range size were not significant. Home-range size was significantly correlated with body mass for females ( $r$

Table 1. Continued.

Site no.	Location	Elevation (m)	Sex	Age <sup>a</sup>	Body mass (g)	No. locations	Sampling duration (day)	Sampling interval (day)	Home-range size (ha)	Source
8	N.Y., 44.2°N, 74.2°W	762	F	Ad	595	270	376	1.4	390	M. K. Brown (N.Y. Dep. Environ. Conserv., unpubl. data)
9	Newf., 48.4°N, 57.6°W	286	M	Ad	936	27	105	4.0	2,750	Bateman (1986)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	681	36	105	3.0	1,770	Bateman (1986)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	750	75	150	2.0	493	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	750	47	135	2.8	353	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	775	23	134	5.6	833	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	750	46	165	3.5	831	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	750	67	173	2.6	424	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	M	Ad	1,325	52	181	3.5	845	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	M	Ad	1,325	135	277	2.0	1,711	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	1,175	50	153	3.0	988	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	1,250	46	89	2.0	426	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	1,250	76	272	3.5	365	Bissonette et al. (1988)
9	Newf., 48.4°N, 57.6°W	286	F	Ad	1,050	91	203	2.2	358	Bissonette et al. (1988)

<sup>a</sup> Juvs < 1 yr, ad  $\geq$  1 yr, U = age unknown.

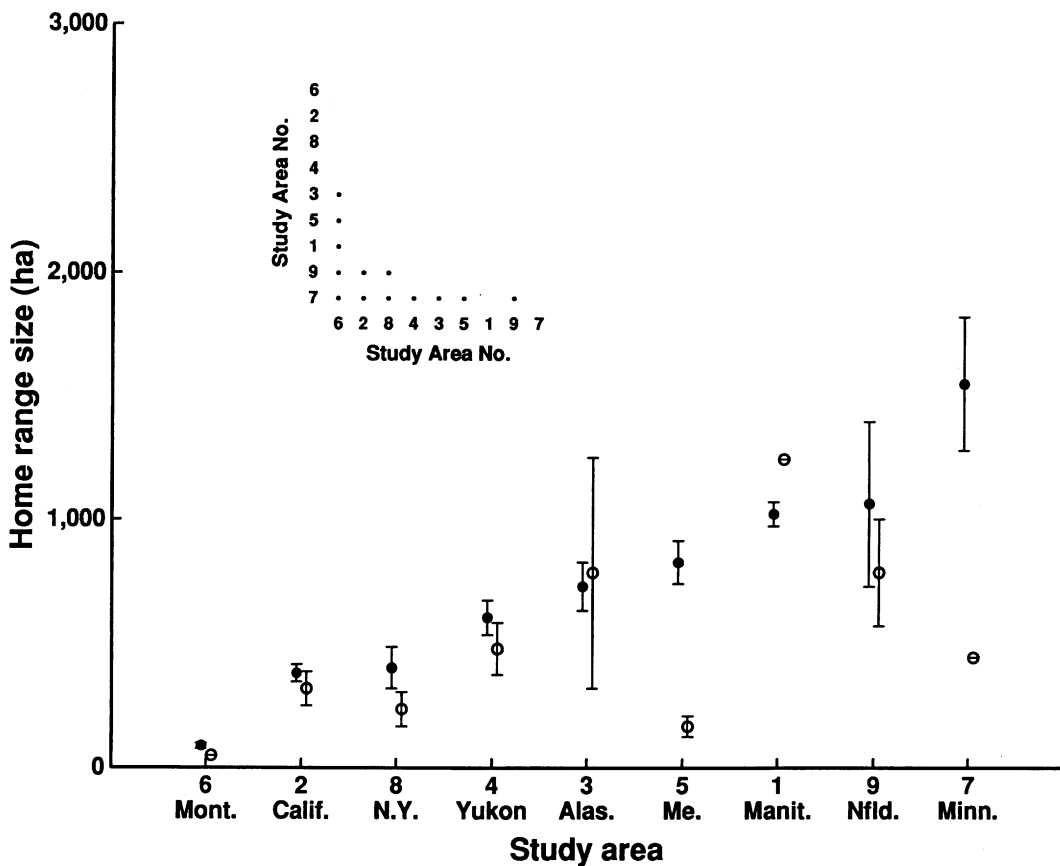


Fig. 1. Mean site-specific home-range size for male (solid circles) and female (open circles) marten from 9 study sites. Bars represent  $\pm 1$  standard error. In inset figure, significant between-site differences ( $P < 0.05$ ) in home-range size for male marten (based on a posteriori Duncan's multiple-range tests) are marked with a dot.

= 0.38,  $P = 0.02$ ,  $n = 32$ ), but not for males ( $P > 0.50$ ).

## DISCUSSION

Although Laundré and Keller (1984) reported no significant differences in between-site comparisons of coyote home-range sizes, we observed that between-site differences in marten home-range sizes were highly significant ( $P < 0.001$ ). Spatial requirements of marten are very large; mean home-range size was about 3 $\times$  that predicted for terrestrial carnivores on the basis of body mass (Lindstedt et al. 1986). Number of locations used to depict a home range and sampling duration were not important sources of variability in published home-range sizes of marten. Only sampling duration was significant in its correlation with home-range size in our preliminary analysis. This may be attributable to shifts in home-range boundaries observed over

long periods. In effect, long periods of sampling may result in multiple home ranges being included in a single depicted home-range perimeter. The lack of a relationship between sampling interval and home-range size suggests that investigators are using sampling intervals greater than those which would cause autocorrelation in telemetry data sets (Swihart and Slade 1985), or that the relationship between sampling interval and home-range size is confounded by other factors.

Territorial spacing has the effect of regulating population density in many terrestrial carnivores. Therefore, hypothesized relationships between habitat quality and population density (Van Horne 1983) may apply to the relationship between home-range size and site conditions in this group. Van Horne (1983) predicted that species in which population density is strongly coupled to habitat quality would be those that

lack a social pattern of dominance interactions where they occur in high densities in high quality habitats, have low reproductive capacity, and are habitat specialists. We hypothesize that there will be a strong relationship between home-range size and site conditions in terrestrial carnivores (e.g., marten) with these same traits.

Home-range size is 1 of the most commonly reported ecological attributes of free-ranging American marten. Including those reviewed in this report, we found 26 studies that described home-range size for marten, 23 of them since 1976. These studies have provided important insights into space requirements and population structure of marten. However, relatively few (Soutiere 1979) related home-range size to site conditions or showed a functional relationship between home-range size and resource abundance (Thompson and Colgan 1987). Studies like these will have increasing importance to managers if the conifer-dominated forests required by marten continue to be shifted toward early successional stages (Thomas et al. 1988). Because home-range size is more easily measured than some other life history traits of marten, site specific home-range sizes hold promise as an indicator of habitat conditions. We encourage others to investigate biological and ecological bases of variability in marten home-range sizes.

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## NUTRIENT AND ENERGY ASSIMILATION OF PREY BY BOBCATS

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**Abstract:** We conducted feeding trials between April and June 1983 to evaluate nutritive and energy values of winter diets of bobcats (*Felis rufus*). We fed snowshoe hares (*Lepus americanus*), white-tailed deer (*Odocoileus virginianus*) meat and viscera, gray squirrels (*Sciurus carolinensis*), and 4 species of small mammals to 4 adult bobcats. Crude protein (62%) and fat content (19%) were similar among diets, except the snowshoe hare diet that was 10 and 15% higher and lower, respectively, than the means. The deer diet was highest in energy content (6.51 kcal/g); the hare diet was lowest (4.66 kcal/g). Significant differences in dry matter digestibility existed between diets; white-tailed deer was the highest (95.7%) and snowshoe hare was the lowest (68.3%). Digestibility of crude protein and fat was  $\geq 80\%$  for all diets, except snowshoe hare (fat = 67%). Metabolizable energy (ME) was significantly different among all diets; the deer diet (5.58 kcal/g dry matter) was highest followed by the squirrel (4.16 kcal/dry matter), small mammal (3.91 kcal/dry matter), and hare (2.9 kcal/dry matter) diets.

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Bobcat management can be enhanced by understanding energetic and nutritive value of prey species. In particular, study of common winter foods in northern regions is important because winter mortality of bobcats is not uncommon, and snow conditions frequently hinder daily movements and alter hunting strategies (McCord 1974, MacLachlan 1981). Documentation of winter diets of northeastern bobcats is fairly

extensive (Pollack 1951, Westfall 1956, Litvaitis et al. 1984); however, little work has been published concerning bobcat nutrition. Golley et al. (1965) examined energy balance of bobcats fed chickens, cottontail rabbits (*Sylvilagus floridanus*), and deer; and Morris et al. (1974) determined digestibility coefficients of dry matter, organic matter, and nitrogen for a commercial feline diet fed to bobcats. Digestibility and energy and nutrient partitioning of prey items can help determine bobcat prey requirements.

Our objective was to determine the nutritive value of 4 important winter foods of northeast-

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